

**Abstract**—Teeth of 71 estuarine dolphins (*Sotalia guianensis*) incidentally caught on the coast of Paraná State, southern Brazil, were used to estimate age. The oldest male and female dolphins were 29 and 30 years, respectively. The mean distance from the neonatal line to the end of the first growth layer group (GLG) was  $622.4 \pm 19.1 \mu\text{m}$  ( $n=48$ ). One or two accessory layers were observed between the neonatal line and the end of the first GLG. One of the accessory layers, which was not always present, was located at a mean of  $248.9 \pm 32.6 \mu\text{m}$  ( $n=25$ ) from the neonatal line, and its interpretation remains uncertain. The other layer, located at a mean of  $419.6 \pm 44.6 \mu\text{m}$  ( $n=54$ ) from the neonatal line, was always present and was first observed between 6.7 and 10.3 months of age. This accessory layer could be a record of weaning in this dolphin. Although no differences in age estimates were observed between teeth sectioned in the anterior-posterior and buccal-lingual planes, we recommend sectioning the teeth in the buccal-lingual plane in order to obtain on-center sections more easily. We also recommend not using teeth from the most anterior part of the mandibles for age estimation. The number of GLGs counted in those teeth was 50% less than the number of GLGs counted in the teeth from the median part of the mandible of the same animal. Although no significant difference ( $P>0.05$ ) was found between the total lengths of adult male and female estuarine dolphins, we observed that males exhibited a second growth spurt around five years of age. This growth spurt would require that separate growth curves be calculated for the sexes. The asymptotic length ( $TL_{\infty}$ ),  $k$ , and  $t_0$  obtained by the von Bertalanffy growth model were 177.3 cm, 0.66, and  $-1.23$ , respectively, for females and 159.6 cm, 2.02, and  $-0.38$ , respectively, for males up to five years, and 186.4 cm, 0.53 and  $-1.40$ , respectively, for males older than five years. The total weight (TW)/total length (TL) equations obtained for male and female estuarine dolphins were  $TW = 3.156 \times 10^{-6} \times TL^{3.2836}$  ( $r=0.96$ ), and  $TW = 8.974 \times 10^{-5} \times TL^{2.6182}$  ( $r=0.95$ ), respectively.

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## Age and growth of the estuarine dolphin (*Sotalia guianensis*) (Cetacea, Delphinidae) on the Paraná coast, southern Brazil

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Until recently the genus *Sotalia* was monospecific (*S. fluviatilis*) and had a marine and a riverine ecotype (da Silva and Best, 1996). Using tridimensional morphometric analyses, Monteiro-Filho et al. (2002) were able to separate it into two distinct species: *Sotalia fluviatilis*, which lives in freshwater, and *Sotalia guianensis*, which lives in the marine environment. Because tucuxi is the vernacular name used for the freshwater species, Rosas and Monteiro-Filho (2002) suggested “estuarine dolphin” as the vernacular name for *S. guianensis*, as previously mentioned by Watson (1988).

Age is important in characterizing population dynamics of mammals. Growth layer groups (GLGs) observed in teeth of mammals have been used to estimate ages, and the greatest progress in this area has occurred with studies carried out on marine mammals (Klevezal, 1980; Hohn et al., 1989). The method consists of counting GLGs found

in the dentine and cement of the animals’ teeth, which are deposited every year in most species (Klevezal, 1996). Calibrating age estimates and identifying accessory layers (not annual) are essential for reliable age determination (Hohn, 1990). Some population parameters are extremely sensitive to errors and age estimate deviations, and the absence of or an inadequate calibration, could lead to incorrect interpretations (Hohn et al., 1989).

Because there is no sexual dimorphism in the body proportions of adult *Sotalia guianensis*, all previous growth studies analyzed both sexes together (Borobia, 1989; Schmiegelow, 1990; Ramos et al., 2000). However, there is evidence of differentiated growth between male and female estuarine dolphins around puberty (Rosas and Monteiro-Filho, 2002), thereby making it necessary to analyze growth separately for the sexes.

The objectives of this paper were 1) to estimate the ages of *S. guianensis*

caught incidentally or stranded on the Paraná coast, Brazil; 2) to give some guidelines to promote reliable age estimates in this species; 3) to describe the growth in body length (cm) according to the ages (years) of male and female estuarine dolphins, by using classical mathematical growth models; and 4) to describe the body-weight–body-length relationship for both sexes of this dolphin.

## Materials and methods

Teeth from 71 individuals of *S. guianensis* (34 males, 28 females and 9 of undetermined sex), incidentally caught or found stranded on the Paraná coast, southern Brazil (25°18'S; 48°05'W–25°5'S8; 48°35'W), from January 1997 to July 1999, were used to estimate age. The total body weight (kg) and standard measurements of individuals were made in accordance to Norris (1961). Total length (cm) was measured in a straight line from the tip of the beak to the central notch of the tail, in an axial projection. The skulls and teeth were collected, prepared, and deposited in the collection of the Instituto de Pesquisas Cananéia (IPEC).

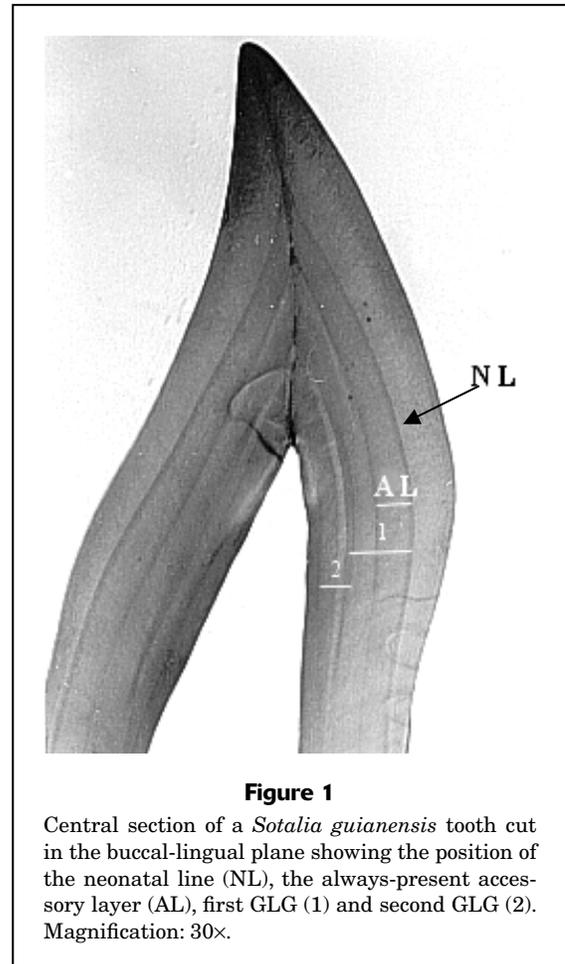
Preparation of the teeth, from the decalcification to the mounting of the slides, was carried out in the Laboratory of Marine Mammals and Marine Turtles of the Department of Oceanography of the Fundação Universidade do Rio Grande (FURG). The method of Hohn et al. (1989) was used, with the following adaptations: 1) decalcification time varied from one hour for newborn or young individuals, up to a maximum of 12.5 hours for old adults, 2) Harris's hematoxylin was used for staining, according to Molina and Oporto (1993), and immersion times of the sections varied from three to six minutes.

Because the absence of a pre-established age estimation model for *S. guianensis*, we tested both anterior-posterior and buccal-lingual planes for cutting teeth. Age estimation was performed by counting GLGs in the dentine. GLGs were defined as being the sequence of a thin nonstained layer, a thick stained layer, and a very thin layer that is strongly stained (very dark). Each complete GLG was assumed to represent one year (Ramos et al., 2000).

Teeth were selected from the middle of the tooth rows. However, to check for differences in age estimation among those positioned along the tooth row, we compared the number of GLGs in teeth from the middle of the tooth row with the number of GLGs in those from the most anterior part of the tooth row of the same animal.

The senior author read teeth slides at least three times during a minimum period of three weeks. Estimated age was taken as the last reading, assuming that reading accuracy improves with practice (Pinedo and Hohn, 2000). Age was estimated without access to biometric and biological data, thereby avoiding reader bias.

By using only central sections or those close by, in which at least 80% of the pulp cavity was exposed (Fig. 1), we obtained the following measurements with an ocular micrometer in a compound microscope: 1) distance (in  $\mu\text{m}$ ) from the neonatal line up to the end of the first GLG in the dentine; 2) distance from the neonatal line to the first



**Figure 1**  
Central section of a *Sotalia guianensis* tooth cut in the buccal-lingual plane showing the position of the neonatal line (NL), the always-present accessory layer (AL), first GLG (1) and second GLG (2). Magnification: 30 $\times$ .

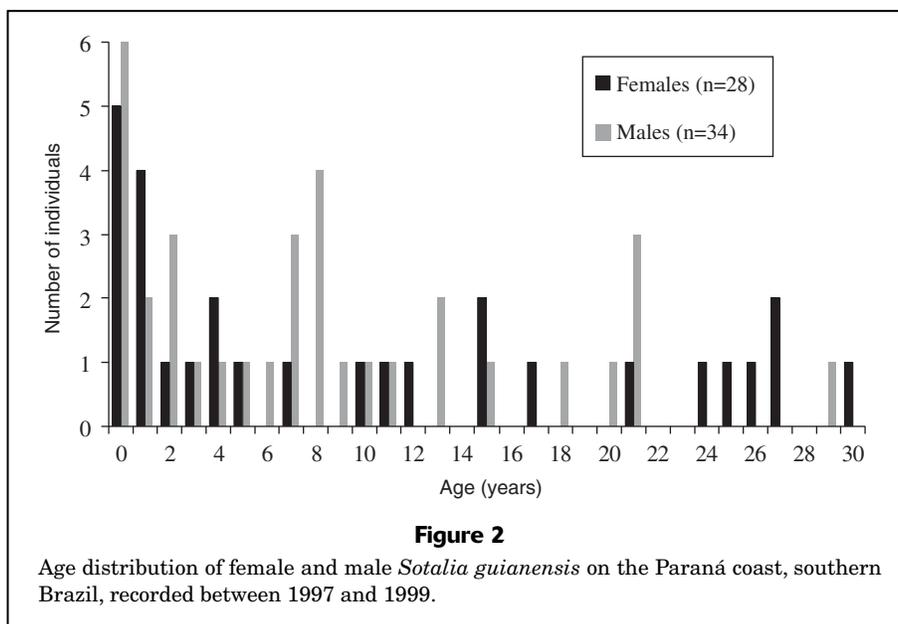
accessory layer in the dentine; and 3) distance from the neonatal line to the second accessory layer in the dentine, if present. All measurements were made perpendicular to the external margin and at the neck of the tooth (an area located between the crown and root of the tooth).

Ages of individuals less than one year were estimated in months, by using as a base the percentage proportion of the mean distance between the neonatal line and the end of the GLG of the first year (Ramos, 1997).

Several models have been created over the years to describe growth, including the von Bertalanffy, Gompertz, logistical, and Richards models. Schnute's generic growth model helps to choose the model which is best adapted to the length and age data of the species studied. Schnute's model (1981) is defined as:

$$Y(t) = \left[ y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{\frac{1}{b}},$$

where  $Y(t)$  represents a measurement (length, weight, volume) at age  $t$ ; variables  $\tau_1$  and  $\tau_2$  are ages of young and old specimens, respectively, and  $y_1$  and  $y_2$  are sizes at these ages. These sizes, together with  $a$  and  $b$ , are the parameters



to be estimated. To define the growth model that would best fit the length and age data of *S. guianensis*, the Schnute model was applied to the length-at-age data.

Growth equations were calculated separately for the sexes, with 34 males and 28 females. Growth model adjustment to the data was made by using the nonlinear iterative Quasi-Newton method, minimizing the residual sum of squares.

Total-weight to total-length relationships were established by using 42 individuals of *S. guianensis* (23 males and 19 females) with the equation

$$TW = \phi \times TL^\theta \quad (\text{Santos, 1978}),$$

where  $TW$  = total weight in kg;

$TL$  = total length in cm;

$\phi = e^a$  ( $e$ =base of the natural logarithm);

$\theta = b$  ( $\theta$  is the length exponent); and finally

$a$  and  $b$  = correlation parameters between the weight and length, obtained by the method of the least square by adjusting the logarithm data of  $TW$  and  $TL$ .

## Results

### Age estimation

The mean distance from the neonatal line to the end of the first GLG was  $622.4 \pm 19.1 \mu\text{m}$  ( $n=48$ ). There is one accessory layer, sometimes two, between the neonatal line and the end of the GLG of the first year. One of them, located at a mean distance of  $248.9 \pm 32.6 \mu\text{m}$  ( $n=25$ ) from the neonatal line, is not always present. The other, which is sometimes very conspicuous at the tip of the tooth, is always present, located at a mean distance of  $419.6 \pm 44.6 \mu\text{m}$

( $n=54$ ) from the neonatal line, and is first observed between 6.7 and 10.3 months of age.

No difference was observed in age estimates of teeth sections orientated in the anterior-posterior and buccal-lingual planes. However, the buccal-lingual orientation made it easier to obtain on-center sections.

The number of GLGs counted in the small teeth from the most anterior part of the tooth row was 50% less than those counted in the teeth from the median part of the mandibles of the same animal.

The proportion of sexes in the sample studied was not significantly different ( $\chi^2=1.39$ ;  $df=1$ ;  $P>0.05$ ). However, among the animals with an age equal to or greater than 24 years ( $n=7$ ), 85.7% were females. The oldest male was 29 years old and the oldest female was 30 years old (Fig. 2).

Age estimates for *S. guianensis* individuals varied from 0 to 30 years. Although the age mode was in the 0 and 1 year classes (Fig. 2), 53.5% of all animals whose ages were estimated were seven years or more. This proportion remained relatively constant between the sexes; 55% of the males and 50% of the females were equal to or greater than seven years.

### Growth

When applied to the present data, Schnute's model indicated that the von Bertalanffy growth equation fitted the length and age data of *S. guianensis* better (Table 1,  $a>0$  and  $b>1$ ; Schnute, 1981). Even though the predictive power of Schnute's model is greater than von Bertalanffy's (see "Explained variance" in Tables 1 and 2), the latter is justified by its historical use, and therefore has a greater value for populational comparison, and incorporates a better understanding of the biological meaning of its variables.

Comparing the total lengths (TL) of the estuarine dolphins of six years or more, we found no significant differ-

ence between the sexes ( $t$ -test,  $P > 0.05$ ). However, it was observed that males possibly exhibit a discontinuity in growth around five years. The existence of a secondary growth spurt around this age was considered to be due to the onset of puberty in this species (Rosas and Monteiro-Filho, 2002), and necessitated the calculation of separate growth curves for each sex. It should be noted that sexual maturity of the dolphins here analyzed was determined by Rosas and Monteiro-Filho (2002) to occur at seven years in males. In order to estimate the fit of a two-step model, the sample was divided into two groups: 1) up to five years (prepuberty) and 2) older than five years (subadult and adults).

The growth parameters obtained for males and females are given in Table 2. The results obtained by Borobia (1989) and Schmiegelow (1990) using the von Bertalanffy growth model are also indicated in Table 2 for comparison. The growth parameters obtained by the analyses of males up to five years of age and those older than five are presented

in Table 3. By dividing the sample in two, the fit of the von Bertalanffy model improved considerably (Tables 2 and 3). The growth curves of *S. guianensis* males and females obtained by the von Bertalanffy model are presented in Figure 3.

The  $t$ -test applied to parameters  $a$  and  $b$  of the weight/length regression equations for males and females revealed a significant difference ( $t=2.25$ ;  $df=38$ ;  $P < 0.05$ ). Therefore, this relationship was analyzed for the sexes separately and the equations obtained were

$$TW = 3.156 \times 10^{-6} \times TL^{3.2836} \quad (\text{males}) (r=0.96)$$

$$TW = 8.974 \times 10^{-5} \times TL^{2.6182} \quad (\text{females}) (r=0.95).$$

## Discussion

### Age estimation

Although there was no difference in the age estimation between teeth orientated in the buccal-lingual and anterior-posterior planes, we recommend the buccal-lingual plane to obtain easier on-center or close-to-center sections, which are essential for accurate age estimates.

The differences found in counting GLGs in teeth from the anterior extremity and the median region of the tooth row of the same animal corroborate the results obtained by Hui (1980) for *Tursiops truncatus*. Therefore, we also do not recommend using teeth from the most anterior part of the mandible for age estimation in *S. guianensis*.

The mean distance between the neonatal line and the end of the first GLG obtained in the present study (622.4  $\mu\text{m}$ ) was approximately double that obtained by Ramos (1997) (297.8  $\mu\text{m}$ ) for estuarine dolphins on the coast of Rio de Janeiro. The differences, however, must be analyzed carefully: the measurements carried out in our study were always made in the neck of the teeth, whereas those made by Ramos (1997) were from the base of the neonatal line. However, the differences may be related to the interpretation of the position of the first annual layer. The accessory layers (non-annual), observed between the neonatal line and the end

**Table 1**

Schnute growth model parameters applied to *Sotalia guianensis* on the Paraná coast, southern Brazil. " $\tau_1$ " and " $\tau_2$ " are predetermined ages in years; " $y_1$ " and " $y_2$ " are estimated sizes at ages  $\tau_1$  and  $\tau_2$ , in cm; " $a$ " and " $b$ " are adimensional parameters. "SQ" represents the residual sum of squares, and "Expl. var." represents the variance of the data explained by the model.

Parameters	Females	Males	All
$\tau_1$	0	0	0
$y_1$	93.11	86.04	89.53
$\tau_2$	28	28	28
$y_2$	181.72	190.45	185.70
$a$	0.14	0.07	0.13
$b$	7.64	9.45	7.86
SQ	1242.35	1898.75	4375.56
Expl. var. (%)	93.47	92.17	92.47
$n$	28	34	71

**Table 2**

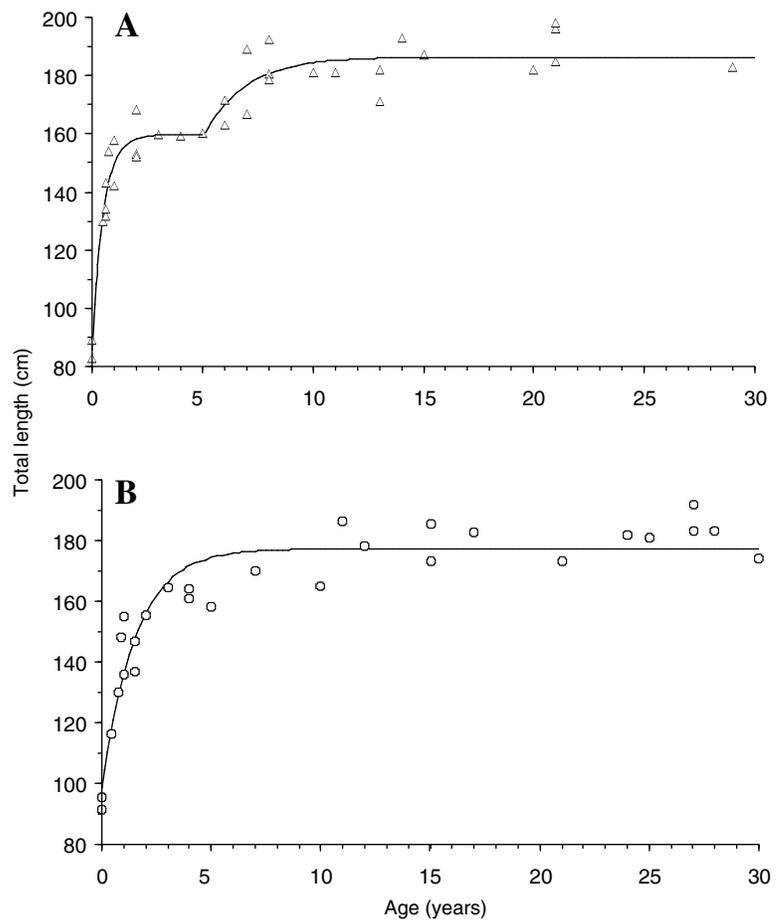
Von Bertalanffy growth model parameters applied to *Sotalia guianensis* on the Paraná coast, southern Brazil, and parameters from the literature. " $TL_\infty$ " = asymptotic length (cm), " $k$ " = growth constant and " $t_0$ " = theoretical age at which the length of the animal is zero. "SQ" represents the residual sum of squares, and "Expl. var." represents the variance of the data explained by the model.

Parameters	Our study			Borobia (1989)	Schmiegelow (1990)
	Females	Males	All		
$TL_\infty$	177.31	179.10	179.53	187.21	182.6
$k$	0.66	1.00	0.79	0.20	0.41
$t_0$	-1.23	0.72	0.95	-4.05	-1.57
SQ	1944.25	3732.30	6942.93	—	—
Expl. var. (%)	89.78	84.61	88.06	—	—
$n$	28	34	71	24	22

of the GLG of the first year, frequently appear in a very conspicuous manner, especially in the tip of the tooth, and can be easily confused with annual layers. The assumption that accessory layers are annual could result in a duplication of the real age of young animals up to two years old, with significant consequences in the interpretations of populational biological parameters (Hohn, 1990). The ideal situation would be that a GLG deposition model already existed for the species being studied, thereby avoiding counting accessory layers as being annual (Hohn et al., 1989). In most odontocete species, including *S. guianensis*, accessory layers do not continue up to the end of the root of the tooth, in contrast to annual layers, which can be seen from the tip to the base of the root of the tooth. However, to identify accessory layers it is necessary that the sections selected for age determination are central, or close to the center of the pulp cavity (Pinedo and Hohn, 2000). Off-center sections can be used for age estimation, but reading errors increase markedly and consequently induce unreliable age estimates (Pinedo and Hohn, 2000).

The reasons for GLG deposition in teeth are unknown (Hohn et al., 1989). However, several reasons have been suggested, including seasonal variations in growth rate, genetic physiological cycles, dietary changes, hormonal influences, and intrinsic factors on the metabolism in general (Boyde, 1980; Klevezal, 1980; Scheffer and Myrick, 1980). Although all these factors could be influential, variations in the diet certainly play a significant role. According to Klevezal (1996), a descriptive record of the dietary changes of an animal during the year should initially be looked for in structures that have a large degree of sensitivity, such as teeth. It is known that dentine reacts to the introduction of fluoride, calciferol and a series of other components in the organism, forming layers with different degrees of mineralization (Klevezal, 1996), which is known as a calcium-traumatic reaction of dentine. Therefore, it is possible to find a record of dietary changes in the dentine, starting from weaning (Klevezal, 1996).

We believe that the accessory layer in the dentine found at approximately 419.6  $\mu\text{m}$  from the neonatal line, could be a record of the end of weaning in the estuarine dolphin. It was observed in all the teeth of individuals older than 6.7 months and could be a hypomineralized layer caused by a reduction of calcium in the body due to the absence of milk in the diet (Klevezal, 1996). The other accessory layer found closer to the neonatal line (mean of 248.9  $\mu\text{m}$ ) was not observed in all animals and the interpretation of this layer remains uncertain. It may be related to the beginning of weaning, as has been suggested for the bottlenose dolphin



**Figure 3**

Growth curve of male (A) and female (B) *Sotalia guianensis* on the Paraná coast, southern Brazil.

**Table 3**

Von Bertalanffy growth model parameters for male *Sotalia guianensis* on the Paraná coast, southern Brazil. " $TL_{\infty}$ " = asymptotic length (cm), " $k$ " = growth constant and " $t_0$ " = theoretical age at which the length of the animal is zero. "SQ" represents the residual sum of squares, and "Expl. var." represents the variance of the data explained by the model.

Parameters	Up to 5 years	More than 5 years
$TL_{\infty}$	159.64	186.41
$k$	2.02	0.53
$t_0$	-0.38	-1.40
SQ	510.99	1013.98
Expl. var. (%)	94.20	50.90
$n$	15	19

(*T. truncatus*) (Hohn<sup>1</sup>). This hypothesis still needs to be confirmed. However, all the *S. guianensis* individuals that were still nursing, but which already had remains of solid food in their stomachs ( $n=5$ ), had only an accessory layer that is closer to the neonatal line—they did not have the layer that we are assuming marks the end of weaning.

According to Rosas (2000), there was no significant difference in incidental catches between mature and immature individuals of *S. guianensis* caught on the coast of Paraná, suggesting a similar vulnerability of young and adult estuarine dolphins to fisheries. Because the animals analyzed in our study were the same ones used by Rosas (2000), this lack of significant difference between mature and immature individuals can suggest a representative age distribution of the individuals analyzed.

Because the maximum estimated age in our study was 30 years, and because the dolphins here analyzed were incidentally caught in fishing nets, it seems reasonable to assume that the longevity of the estuarine dolphin may be 30–35 years. This hypothesis is also corroborated by the study carried out by Ramos (1997) with *S. guianensis* on the coast of Rio de Janeiro State (southeastern Brazil). Although the age of the oldest male observed in our study was 29 years, the frequency of males older than 21 years was less than 3%, which is extremely low when compared with the frequency of 21.5% for females older than 21 years. These results suggest a greater life expectancy for females, which is also corroborated by a study carried out by Ramos (1997) in Rio de Janeiro.

## Growth

The use of Schnute's model is helpful in deciding which growth model should be used. Even though the researcher can usually decide which model is most appropriate by looking at the data, subtle differences in data distribution could cause one or another model to be more adequate. Use of a generic model allows this choice without intervention of the researcher and avoids any unconscious bias towards or against any model.

The discontinuity of growth in male *S. guianensis* in our study could have been due to the small sample size or may have been due to a second growth spurt, which has already been observed in the total length of *Stenella attenuata* (Perrin et al., 1976), *Lissodelphis borealis* (Ferrero and Walker, 1993), and *Phocoenoides dalli* (Ferrero and Walker, 1999), and in the weight of male *Tursiops truncatus* (Cockroft and Ross, 1990). The  $k$  value obtained for male *S. guianensis* up to five years was very high, meaning that asymptotic length in this phase of life was reached quickly. The cessation of growth exhibited by the model for males up to 5 years probably is not true in the biological sense but could be an artifact created by the model and the small sample size. Most probably there is a marked reduction in growth with the start of sexual maturation and a greater investment in the weight or reproductive apparatus (or

both). The hypothesis of a greater investment in weight is supported by the observed difference in the weight-length coefficient between males and females. Additionally, sexual investment of male estuarine dolphins is very high—testes of adult males can reach up to 32 cm in length and weigh up to 3.3% of the total body weight (Rosas and Monteiro-Filho, 2002).

After the secondary growth spurt in males, the final asymptotic length did not differ very much from that in females. Previous growth studies carried out by Borobia (1989), Schmiegelow (1990), and Ramos et al. (2000) with the estuarine dolphin did not mention the existence of a second growth spurt in males, possibly because the authors did not analyze the growth of males and females separately. According to Ramos et al. (2000), male and female data were combined because of the absence of sexual dimorphism in the body size of adults of this species.

Borobia (1989) and Schmiegelow (1990), who also used the von Bertalanffy model, obtained different values for the growth equation parameters (Table 1). The sample used by Borobia (1989) did not have many individuals in ages 1 and 2, and none in the 0 age class. The absence of animals that “anchor” the beginning of the curve could result in low estimates of  $k$  and  $t_0$ . Additionally, Borobia (1989) examined individuals from different locations along the distribution of the species and thus did not take into consideration possible geographical variations. The results obtained by Schmiegelow (1990) are similar to those of our study, probably because both of them used animals from the same region.

Ramos et al. (2000) analyzed the growth of *S. guianensis* using the Gompertz growth model and obtained an asymptotic length (191.7 cm) which was much greater than that obtained in our study and in previous studies (Borobia, 1989; Schmiegelow, 1990) (Table 1). This difference could be due to 1) the small number of individuals older than 12 years ( $n=3$ ) in their sample; or 2) a difference in asymptotic lengths between southeastern and southern Brazil populations. Similar differences have been observed between asymptotic lengths of *Pontoporia blainvillei* from Rio de Janeiro (southeastern Brazil) and São Paulo and Paraná (same area of the present study), where larger individuals were found in Rio de Janeiro (Ramos et al., 2000; Rosas, 2000). Therefore, it is possible that environmental variables could be responsible for larger sizes in the area studied by Ramos et al. (2000), both for *S. guianensis* and for *P. blainvillei*.

Although no significant difference was observed in the asymptotic length between adult males and females, the differentiated growth in time between the two sexes is probably responsible for the difference observed in the weight-length relationship.

In most species, the length exponent ( $\theta$ ) of the weight-length relationship is usually close to 3 (Santos, 1978). The estimated values of this exponent for the estuarine dolphin (3.2 for males and 2.6 for females) suggest that the longitudinal and transversal body growth in this species follows a similar pattern.

Our results suggest that it is important to study growth by analyzing the sexes separately, because there may be differential growth between the sexes before the adult age.

<sup>1</sup> Hohn, A. A. 1999. Personal commun. Beaufort Laboratory, Southeast Fisheries Science Center, National Marine Fisheries Service, 101 Privers Island Road. Beaufort, NC 28516-9722.

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## Literature cited

- Borobia, M.  
1989. Distribution and morphometrics of South American dolphins of the genus *Sotalia*. MSc. thesis, 81 p. McDonald College, McGill University. Montreal, Quebec, Canada.
- Boyde, A.  
1980. Histological studies of dental tissues of Odontocetes. In Age determination of toothed whales and sirenians (W. F. Perrin and A. C. Myrick, eds.), p. 65–87. Rep. Int. Whal. Comm., Special Issue 3.
- Cockcroft, V. G., and G. J. Ross.  
1990. Age, growth, and reproduction of bottlenose dolphins *Tursiops truncatus* from the east coast of Southern Africa. Fish. Bull. 88:289–302.
- da Silva, V. M. F., and R. C. Best.  
1996. *Sotalia fluviatilis*. Mammalian Species 527:1–7.
- Ferrero, R. C., and W. A. Walker.  
1993. Growth and reproduction of the northern right whale dolphin, *Lissodelphis borealis*, in the offshore water of the North Pacific Ocean. Can. J. Zool. 71:2335–2344.  
1999. Age, growth and reproductive patterns of Dall's porpoise (*Phocoenoides dalli*) in the Central North Pacific Ocean. Mar. Mamm. Sci. 15(2):273–313.
- Hohn, A. A.  
1990. Reading between the lines: Analysis of age estimation in dolphins. In The Bottlenose dolphin (S. Leatherwood and R. R. Reeves, eds.), p. 575–585. Academic Press, New York, NY.
- Hohn, A. A.; M. D. Scott, R. S. Wells, J. C. Sweeney, and A. B. Irvine.  
1989. Growth layers in teeth from known-age, free-ranging bottlenose dolphins. Mar. Mamm. Sci. 5 (4):315–342.
- Hui, C. A.  
1980. Variability of dentine deposition in *Tursiops truncatus*. Can. J. Fish. Aquat. Sci. 37:712–716.
- Klevezal, G. A.  
1980. Layers in the hard tissues of mammals as a record of growth rhythms of individuals. In Age determination of toothed whales and sirenians (W. F. Perrin and A. C. Myrick, eds.), p. 89–94. Rep. Int. Whal. Comm. Special Issue 3.  
1996. Recording structures of mammals. Determination of age and reconstruction of life history, 274 p. A.A. Balkema, Rotterdam, Netherlands.
- Molina, D. M., and J. A. Oporto.  
1993. Comparative study of dentine staining techniques to estimate age in the Chilean Dolphin, *Cephalorhynchus eutropia* (Gray, 1846). Aquat. Mamm. 19 (1):45–48.
- Monteiro-Filho, E. L. A., L. R. Monteiro, and S. F. dos Reis.  
2002. Skull shape and size divergence in the dolphins of the genus *Sotalia*: a tridimensional morphometric analysis. J. Mamm. 83 (1):125–134.
- Norris, K. S.  
1961. Standardized methods for measuring and recording data on the smaller cetaceans. J. Mamm. 42 (4):471–476.
- Perrin, W. F., J. M. Coe, and J. R. Zweifel.  
1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull. 74(2):229–269.
- Pinedo, M. C., and A. A. Hohn.  
2000. Growth layer patterns in teeth from the franciscana, *Pontoporia blainvillei*: developing a model for precision in age estimation. Mar. Mamm. Sci. 16 (1):1–27.
- Ramos, R. M. A.  
1997. Determinação de idade e biologia reprodutiva de *Pontoporia blainvillei* e da forma marinha de *Sotalia fluviatilis* (Cetacea: Pontoporiidae e Delphinidae) no norte do Rio de Janeiro. M.Sc. thesis, 95 p. Universidade Estadual do Norte Fluminense. Campos dos Goytacazes, Rio de Janeiro, Brasil.  
2000. Growth parameters of *Pontoporia blainvillei* and *Sotalia fluviatilis* (Cetacea) in northern Rio de Janeiro, Brazil. Aquat. Mamm. 26 (1):65–75.
- Rosas, F. C. W.  
2000. Interações com a pesca, mortalidade, idade, reprodução e crescimento de *Sotalia guianensis* e *Pontoporia blainvillei* (Cetacea, Delphinidae e Pontoporiidae) no litoral sul do Estado de São Paulo e litoral do Estado do Paraná, Brasil. Ph.D. diss., 145 p. Universidade Federal do Paraná. Curitiba, PR, Brasil.
- Rosas, F. C. W., and E. L. A. Monteiro-Filho.  
2002. Reproduction of the estuarine dolphin (*Sotalia guianensis*) on the coast of Paraná, southern Brazil. J. Mamm. 83(2):507–515.
- Santos, E. P.  
1978. Dinâmica de populações aplicada à pesca e piscicultura, 129 p. Editora de Humanismo, Ciência e Tecnologia "HUCITEC" Ltda, São Paulo.
- Scheffer, V. B., and A. C. Myrick.  
1980. A review of studies to 1970 of growth layers in the teeth of marine mammals. In Age determination of toothed whales and sirenians (W. F. Perrin and A. C. Myrick, eds.), p. 51–63. Rep. Int. Whal. Comm., Special Issue 3.
- Schmiegelow, J. M. M.  
1990. Estudo sobre cetáceos odontocetes encontrados em praias da região entre Iguape (SP) e Baía de Paranaguá (PR) (24°42'S–25°28'S) com especial referência a *Sotalia fluviatilis* (Gervais, 1853) (Delphinidae). M.Sc. thesis, 149 p. Universidade de São Paulo, Instituto Oceanográfico, São Paulo.
- Schnute, J.  
1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38:1128–1140.
- Watson, L.  
1988. Whales of the world. A handbook and field guide to all the living species of whales, dolphins and porpoises, 302 p. Hutchinson, London.